GEOGRAPHIC LIMITS AND LOCAL ZONATION: THE BARNACLES *SEMIBALANUS (BALANUS)* AND *CHTHAMALUS* IN NEW ENGLAND

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ABSTRACT

The interactions between the intertidal barnacles *Semibalanus (Balanus) balanoides* and *Chthamalus fragilis* were examined in order to determine whether the factors which influence local zonation in the intertidal also contribute to the establishment of geographic limits.

Both physical and biotic factors influence intertidal zonation at the northern limit of *Chthamalus* in New England. On sloping surfaces *Semibalanus* died at all shore levels higher than mid tide level, apparently as a result of desiccation associated with high summer temperatures. *Chthamalus* settlement occurred at all shore levels above mean tide level, and postsettlement mortality apparently restricts *Chthamalus* to high shore locations where *Semibalanus* growth and survival is inhibited. North of the northern limit of *Chthamalus*, *Semibalanus* does not suffer summer heat death, so it occupies the zone where *Chthamalus* would have a refuge from competition further south.

The northern limit of *Chthamalus* is set not by factors directly related to cold acting on *Chthamalus*. Rather the northern limit appears to be set by cold which allows the dominant competitor to exclude *Chthamalus* from its refuge zone. South of the northern limit the competitor, *Semibalanus,* is excluded from the high shore by high summer temperatures.

INTRODUCTION

One of the goals of ecology is to determine the mechanisms responsible for the patterns of distribution and abundance of organisms. The rocky intertidal zone has been used very successfully to make experimental tests of a wide variety of hypotheses about the organization of communities and the dynamics of assemblages of species. Much of this work has been designed to elucidate patterns of local distribution and abundance, rather than large scale geographic patterns. Here I examine whether the same mechanisms that control local zonation are responsible for large scale geographic patterns, those of geographic limits of species.

The strong physical gradient in the intertidal zone was long considered to be fully responsible for the zonation patterns observed. Upper and lower limits of distribution were thought to be set by physiological tolerances (Colman, 1933; Hewatt, 1937; Doty, 1946). Upper limits on the shore are now known to be generally determined by physical factors. Foster (1969) and Hatton (1938) demonstrated that barnacles die if transplanted above their usual shore zone, and that both heat and moisture influence the rate of death. There is little field evidence that intolerance of submersion sets the lower limit of marine species in the intertidal zone. The

majority of the evidence is consistent with the hypothesis (Connell, 1961a, b) that local lower limits are set by interactions with predators or competitors (*e.g.,* reviews by Connell, 1972; Paine, 1974; Menge, 1976; Lewis, 1977; Lubchenco and Menge, 1978; Schonbeck and Norton, 1978; Lubchenco, 1980).

Geographic limits have been correlated with physical conditions in much the same way as have local zonation patterns. Hutchins (1947) hypothesized that the most likely factors limiting geographic distribution were lethal temperatures for adults and what he termed critical temperatures within which reproduction is successful. In some cases the lethal physiological limits of species as determined in laboratory studies correspond to geographic limits (*e.g.,* Vernberg and Tashian, 1959; Vernberg and Vernberg, 1967), but in other cases, geographic ranges are narrower than predicted from studies of lethal limits (*e.g.,* Barnes, 1958; Southward, 1958). Since local zonation is not entirely controlled by lethal physiological limits, and biotic interactions are often locally dominant, it is likely that biotic interactions also play an important role in determining geographic limits.

In this paper I discuss biotic and physical factors which appear to strongly influence the northern geographic limit of the intertidal barnacle *Chthamalus fragilis* on the Atlantic coast of North America. *Chthamalus fragilis* ranges from the Caribbean to Cape Cod (Dando and Southward, 1980). At the northern end of its distribution it is restricted to a narrow zone at the upper levels of the intertidal. Below this zone lives an arctic barnacle species *Semibalanus balanoides.* This type of zonation is also found near the northern limit of *Chthamalus* in Scotland, where Connell (1961a) demonstrated that the upper shore limit of *Chthamalus* was set by desiccation and the lower shore limit was set by competition with *Semibalanus.* *Semibalanus* was renamed by Newman and Ross (1976); it is referred to as *Balanus balanoides* in all previous literature.

MATERIALS AND METHODS

This study was carried out 100 km north and 150 km south of the recorded northern limit of *Chthamalus* on Cape Cod, Massachusetts. The northern site was East Point, Nahant, Massachusetts (42 25 N, 70 54 W), near the Northeastern University Marine Science Institute. At this location only *Semibalalanus* is present. Here, the tidal range is approximately 3.5 meters. The southern sites were the Yale University Peabody Museum Field Station at Guilford, Connecticut (41 16 N, 72 44 W), and nearby Horse Island in the Long Island Sound (41 15 N, 72 45 W). At these sites, both *Semibalanus* and *Chthamalus* coexist. The tidal range at these sites is approximately 1.9 meters. *Semibalanus* settles at all sites between March and May, and *Chthamalus* settles in Connecticut in August and September.

The zonation patterns of *Semibalanus* and *Chthamalus* were quantified by transects of contiguous 0.5 m × 0.5 m quadrats, which were photographed with a 70 mm camera held perpendicular to the shore with a focal framer. Permanent quadrats were marked with stainless steel screws set in the corners. Percent cover of live and dead organisms was estimated by placing a transparent plastic sheet with 49 uniformly plotted dots on its surface over enlargements of the photographs. Percent cover was then estimated by counting the number of dots overlying each species (*e.g.,* Menge, 1976). Transects were established in a variety of locations in order to determine the influence of shore orientation and aspect. Heights of the marker screws relative to mean low water were estimated by the tables in the Tide Tables (NOAA, 1982). Percent cover data are based on samples taken in August and October.

Settlement of *Chthamalus* in the absence of *Semibalanus* was estimated by removing *Semibalanus* with a paint scraper in a checkerboard pattern in permanently marked quadrats. In this way *Semibalanus* removals were performed at all shore levels. Removals were performed in August 1982, at the beginning of the *Chthamalus* settlement season. Settlement was measured in mid October, 1982, by counting newly settled spat in 4 cm × 4 cm quadrats in the field.

RESULTS

In Connecticut, *Chthamalus* occupies a narrow zone near mean high water of neap tides (Figs. 1–4). The zonation is strongly influenced by slope and aspect. On north-facing vertical surfaces, *Chthamalus* occupies a very narrow zone on the high shore (Fig. 1). Maximum percent cover is 50% near mean high water of neap tides (Fig. 1). Below this level, *Semibalanus* occupies 100% of the space (Fig. 1). On south-facing vertical surfaces, *Chthamalus* occupies a wider zone. Its upper shore limit is similar to that on north facing surfaces, but its lower limit is 25 cm lower (Fig. 1). Its maximum percent cover is almost 100% on west facing vertical surfaces (Fig. 1). *Semibalanus* occupies 100% of the space below *Chthamalus,* down to mid-tide level. Below this zone, predation by the gastropod *Urosalpinx* apparently reduces the percent cover of *Semibalanus. Urosalpinx* densities are as high as 200 per square meter at mean low water of neap tides. On horizontal surfaces, *Chthamalus* occupies a wider zone, and *Semibalanus* reaches its abundance peak very low on the shore (Fig. 1). In the region below the *Chthamalus* zone, there was evidence of widespread death of small *Semibalanus* (3 mm to 5 mm basal diameter) on sloping and horizontal surfaces. Settlement of *Semibalanus* occurred throughout the intertidal zone in March, and the newly settled individuals died in mid-summer on much of the shore above mid-tide level. The dead individuals were tightly crowded, indicating that the *Semibalanus* settlement had occupied almost 100% of the space below the *Chthamalus* zone. The most likely cause of death of small individuals on horizontal surfaces is desiccation related to summer high temperatures. There was no evidence of *Chthamalus* death from desiccation.

More evidence of *Semibalanus* death resulting from high temperatures may be seen in the zonation on a surface with a 70° slope which has a slow drip from a deep crevice in the rock surface. Two transects were enumerated within the permanent 0.5 m × 0.5 m quadrats. The transects were 0.25 m apart. One ran through the area with the water drip, and the parallel transect was dry. In the area with the water drip, the upper shore limit of *Semibalanus* was 25 cm higher than in the adjacent dry transect (Fig. 2). In the dry transect there were tightly crowded small dead *Semibalanus* at the same shore level where individuals survived in the damp location.

The influence of shade is clearly seen in a series of three parallel transects set up close to the laboratory dock. In the partial shade of the dock the *Chthamalus* zone is very narrow. *Semibalanus* occupies most of the space in the mid shore, and *Fucus* occupies all space at mid tide level and below (Fig. 3A). In a parallel transect 0.5 meters away from the dock, there is less shade, the *Chthamalus* zone is wider, and *Semibalanus* occupies a narrower zone, with *Fucus* at mid tide level (Fig. 3B). In a third parallel transect 0.5 meters farther still from the dock, there is little shade, the *Chthamalus* zone is even wider, and the upper shore limit of *Semibalanus* is 0.5 meters lower than it was in full shade (Fig. 3C).

The summer heat death documented here was common on all sloping shores near the Yale Field station, and on the island shores visible en route to Horse Island
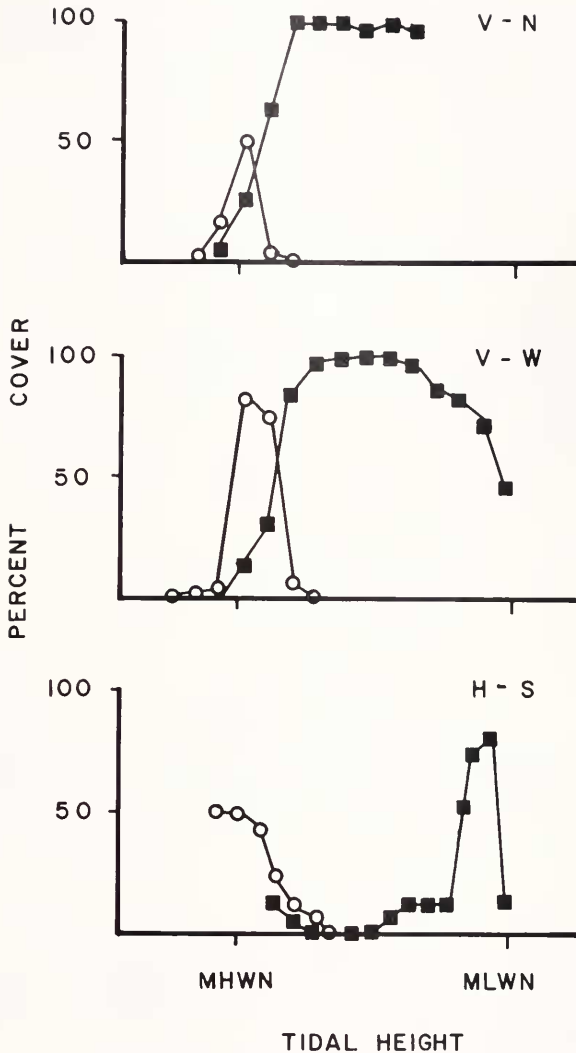
FIGURE 1. Percent cover of *Chthamalus* (open circles) and *Semibalanus* (solid squares) as a function of tidal height on transects at Horse Island, Connecticut. Tide levels are mean high water of neap tides (MHWN) and mean low water of neap tides (MLWN). Top panel is a vertical north facing surface (V-N), center panel is a vertical west facing surface (V-W), bottom panel is a 10 degree slope facing south (H-S).

in Long Island Sound. The total length of shoreline observed exceeded 5 kilometers. This appeared to be a widespread mortality event on the high shore.

In order to test the hypothesis that the lower limit of *Chthamalus* was set by postsettlement mortality associated with the presence of *Semibalanus*, a series of *Semibalanus* removals were set up at all shore levels. Smothered individuals of *Chthamalus* were encountered several times during the process of scraping *Semibalanus* off the rock during establishment of the *Semibalanus* removals. *Chthamalus* subsequently settled in the *Semibalanus* removal areas. The heaviest settlement of
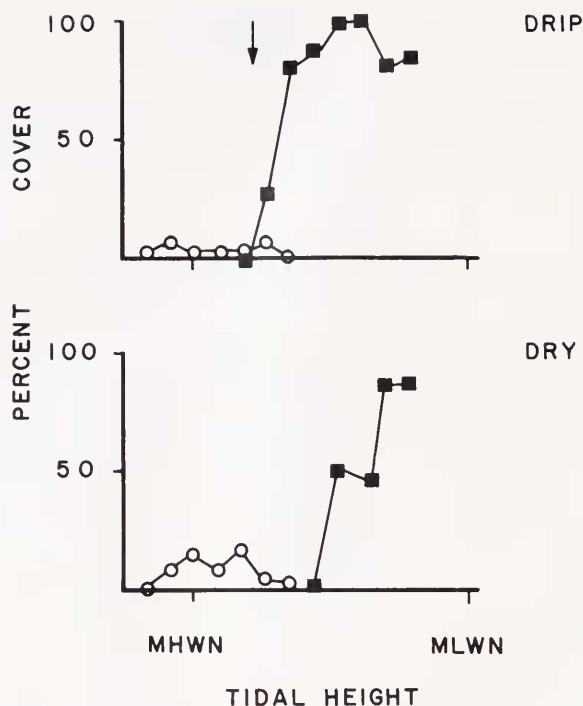
FIGURE 2. Percent cover of *Chthamalus* (open circles) and *Semibalanus* (solid squares) as a function of tidal height on transects at the Yale Field Station in Guilford, Connecticut. Tide levels marked as in Figure 1. The two panels are from parallel transects 25 cm apart. Upper panel transect has water seepage from a deep crevice in the rock surface located at the position of the arrow. Lower panel transect is dry. Note the upward displacement of *Semibalanus* in the damp area below the water seepage.

Chthamalus on vertical surfaces was near mid tide level, in the zone where individuals usually die as a result of overgrowth by *Semibalanus* (Fig. 4). There was very little settlement in the *Chthamalus* zone itself (Fig. 4). On horizontal surfaces, settlement was most intense near mid tide level, in the zone where *Semibalanus* died as a result of summer heat (Fig. 4).

Semibalanus removals were established in August, and settlement of *Chthamalus* occurred prior to the October samples (Fig. 4). These sites were surveyed at the end of April, at the height of the *Semibalanus* settlement season. *Semibalanus* had settled at densities in excess of 50 per square centimeter. In the vertical sites (Figs. 1,4), at all but the highest shore levels, *Chthamalus,* in the *Semibalanus* removal quadrats, were overgrown by newly settled 2-week-old *Semibalanus.* When the nearly 100% cover of newly settled *Semibalanus* was removed with a toothbrush, live *Chthamalus* were found beneath it. Presumably these totally smothered *Chthamalus,* although tolerant of desiccation (Foster, 1971a), would die within a few weeks with no direct access to food, water, or oxygen.

Approximately 5% of the live *Chthamalus* (approximately 5 mm diameter) were being undercut (*sensu* Connell, 1961a), lifted from the substratum, and expelled from the growing surface of *Semibalanus* spat (approximately 1 mm diameter). No crushing of *Chthamalus* by newly settled *Semibalanus* was observed. *Semibalanus* spat were completely occluding the opercular valves of the majority of *Chthamalus* in the zone where the adults of the two species co-occur, yet there was no settlement
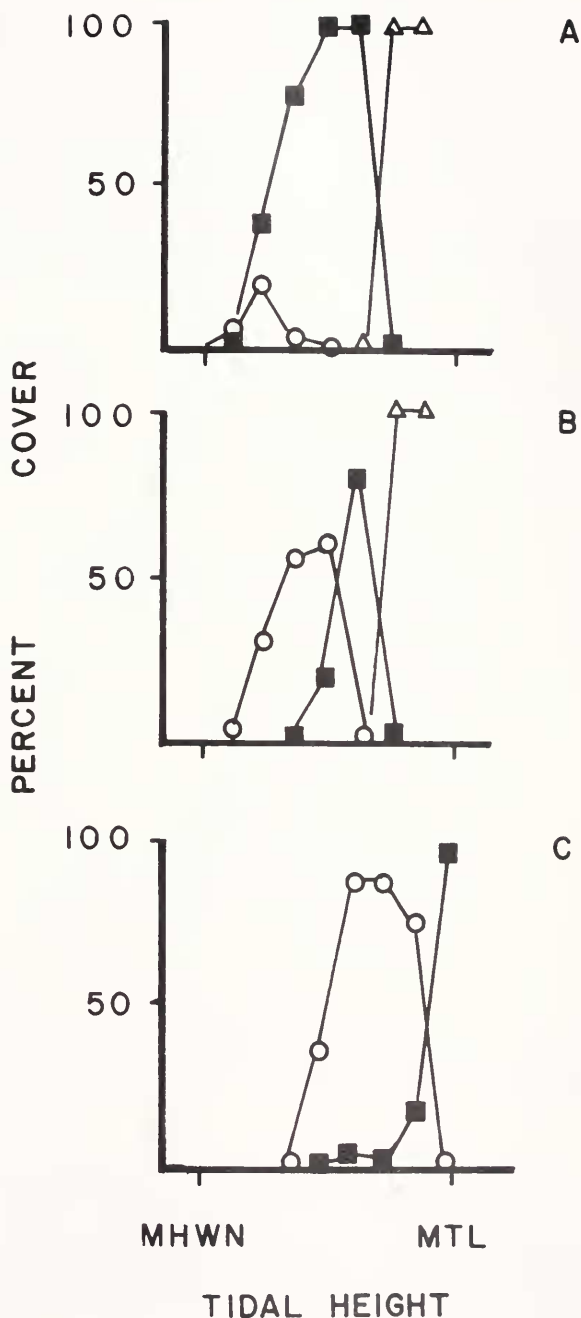
FIGURE 3. Percent cover of *Chthamalus* (open circles) and *Semibalanus* (solid squares) and *Fucus* (open triangles) as a function of tidal height on transects at the Yale Field Station in Guilford, Connecticut. Tide levels are mean high water of neap tides (MHWN) and mean tide level (MTL). The panels are from three parallel transects separated from one another by 0.5 m. Panel A is adjacent to the laboratory dock and is shaded for most of the day. Panel B is 0.5 meters farther from the dock and has more exposure to sun. Panel C is 0.5 meters still farther from the dock and is exposed to sun for more than half of the day. Shore has a 45 degree slope and faces east. Note the downward displacement of the *Semibalanus* upper shore limit as the shore receives more sun.
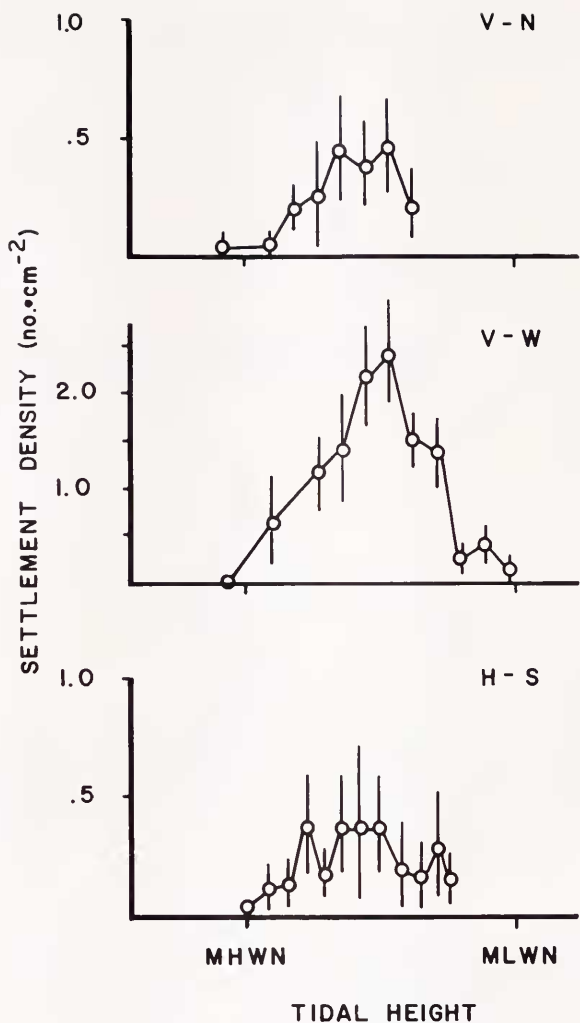
FIGURE 4. Settlement density of *Chthamalus* in numbers per cm² in *Semibalanus* removals. Means and standard deviations from 5 to 10 replicate counts of 4 cm × 4 cm quadrats are reported as a function of tidal height. Symbols and locations are as in Figure 1.

on the opercular valves of adjacent *Semibalanus* individuals. In sites where *Semibalanus* settlement was less intense (shore sites used for Figs. 2 and 3), *Semibalanus* had not yet overgrown *Chthamalus* but were likely to do so by June or July.

These results indicate that *Chthamalus* is capable of settlement and survival for at least 8 months (August through April) at mid-tide level in the absence of *Semibalanus*. Postsettlement mortality as a result of competition with *Semibalanus* is the most likely mechanism causing the restriction of *Chthamalus* to the high shore. Although *Chthamalus* settles most heavily in the mid-shore, it survives only in its refuge from competition high on the shore, where *Semibalanus* is restricted by desiccation. Postsettlement mortality of *Chthamalus* is likely to be very intense in spring when *Semibalanus* settlement occurs, thereby smothering *Chthamalus*.

In the northern site, beyond the northern limit of *Chthamalus,* zonation varies as a function of slope and aspect, but there was no evidence of the widespread heat death that characterized sloping shores in Connecticut. On vertical surfaces, the upper shore limit of *Semibalanus* is higher on north-facing localities than in south-facing shores (Fig. 5). On sloping surfaces *Semibalanus* survives from mean high water of neap tides down to mid-tide level, where it is excluded by competition with the mussel *Mytilus* (Fig. 5). In the seven summers for which I have data on the distribution and abundance of barnacles (1976–1982), *Semibalanus* populations in northern Massachusetts have never suffered summer heat death of the kind documented from the Connecticut shore in 1982 (Wethey, 1979; personal observation).
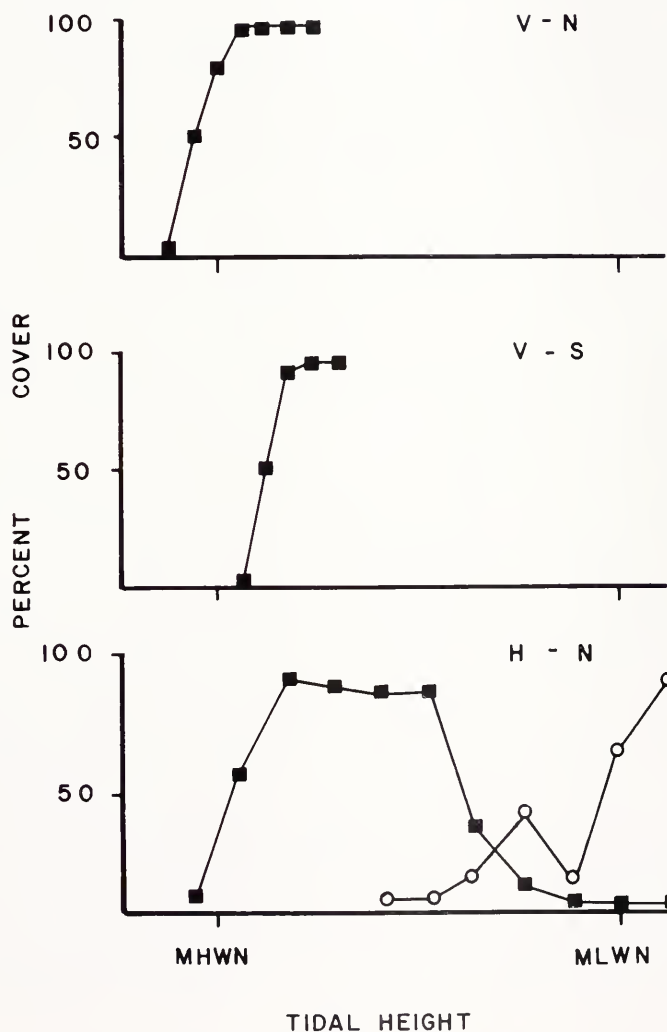

FIGURE 5. Percent cover of *Semibalanus* (solid squares) and *Mytilus* (open circles) as a function of tidal height on transects at Nahant, Massachusetts. Tide levels are as in Figure 1. Top panel is a vertical north facing surface (V-N), center panel is a vertical south facing surface (V-S), bottom panel is a 30 degree slope facing northwest (H-N).

DISCUSSION

This study was set up to determine whether the factors which influence local zonation in the intertidal might also contribute to the establishment of geographic limits. Both physical and biotic factors appear to influence zonation at the northern limit of *Chthamalus* in New England. The upper shore limit of *Semibalanus* is apparently set by desiccation associated with high summer temperatures. In damp or shaded locations, *Semibalanus* occupies the shore up to mean high water of neap tides (Figs. 1–3). In sunny locations the upper shore limit of *Semibalanus* is lower than in shaded locations (Figs. 1–3). On sloping surfaces *Semibalanus* died apparently as a result of desiccation at all shore levels higher than mean tide level (Figs. 1, 2). *Chthamalus* survives in locations where *Semibalanus* fails to persist (Figs. 1–3). Settlement of *Chthamalus* occurs at all shore levels down to mean tide level (Fig. 4), and apparently post-settlement-mortality subsequently limits *Chthamalus* to locations where *Semibalanus* growth is restricted. Warmer, drier sites have wider *Chthamalus* zones because these locations are apparently too hot or dry for *Semibalanus* (Figs. 1–3). These same factors may also be important in setting the northern limit of *Chthamalus*. North of the northern limit of *Chthamalus, Semibalanus* does not suffer summer heat death, so it occupies the zone where *Chthamalus* would have a refuge from competition further south (Fig. 5). In the absence of a refuge, any *Chthamalus* larvae that settle on the high shore are likely to be crushed or overgrown by *Semibalanus*. This in turn reduces the pool of adult *Chthamalus* which contribute larvae to the plankton. The reduced number of larvae available for settlement and the reduced settlement success as a result of competition presumably combine to restrict *Chthamalus* from more northern locations. Thus the northern limit of *Chthamalus* is not set by factors which are directly related to cold acting on *Chthamalus*. Rather, the northern limit appears to be set by cold which allows the dominant competitor to exclude *Chthamalus* from its refuge zone. South of the northern limit the competitor, *Semibalanus,* is excluded from the high shore by high summer temperatures. The northern limit of *Chthamalus* is likely to be more strongly influenced by competition between *Semibalanus* and *Chthamalus* than by direct physiological limitation of *Chthamalus* itself.

These results are consistent with those of Connell (1961a), who documented the importance of competition in setting local limits of zonation in *Semibalanus balanoides* and *Chthamalus* near the northern limit of *Chthamalus* in Scotland. *Chthamalus* was successful in the zone where *Semibalanus* suffered mortality from desiccation. *Chthamalus* settled at shore levels below the zone where adults survived. Post-settlement mortality as a result of competition with *Semibalanus* limited *Chthamalus* to the high shore (Connell, 1961a). Barnes (1956) maintained *Chthamalus* (on stones from Connell's 1961a experiments) under conditions of total submersion on a raft for two years. He found that the growth rate under these conditions was equivalent to that of individuals in the intertidal zone. He reported that post-settlement mortality of *Chthamalus* as a result of space competition with *Semibalanus* restricted it from the low shore: on the raft "a 6-month-old *Chthamalus* settlement (2 mm long) was obliterated in a few weeks by a moderate spat fall of [*Semi*]*Balanus* and full grown *Chthamalus* (9–15 mm) were completely overgrown in 2 months."

All of these results are consistent with the hypothesis that competition with *Semibalanus* is a major determinant of local distribution and abundance of *Chthamalus*. The restriction of *Semibalanus* to shaded habitats in more southern locations has been reported by Barnes (1958) for Woods Hole, where summer heat apparently

killed off 95% of 5 mm basal diameter individuals on south-facing and horizontal surfaces in 1956. On north-facing surfaces mortality was only 50% in the same period (Barnes, 1958). These individuals were about the same size as those found dead in the present study (3 mm basal diameter). Several authors (Southward and Crisp, 1956; Lewis, 1957, 1964; Crisp and Southward, 1958; Bowman, 1983) have reported effects of shore slope and aspect similar to those described here. Near its northern limit in Scotland, *Chthamalus* is more common on south-facing vertical surfaces which dry out at low tide, while *Semibalanus* dominates at the same tide levels in more horizontal locations which remain wet. The most favorable location for *Semibalanus* in southwest England is under rocks and overhangs (Southward and Crisp, 1954). *Semibalanus* in southwest England is almost completely absent from the south facing coast, is rare on the west-facing portion, and is abundant on the north-facing section (Crisp and Southward, 1958). On the north Cornwall coast, *Semibalanus* becomes rare along the eastern section where more of the coast faces west (Crisp and Southward, 1958). Summer heat death of *Semibalanus* in 1976 in northern Scotland resulted in a lowering of the lower limit of *Chthamalus* on those shores (Bowman, 1983). These distribution patterns are consistent with the hypothesis that *Semibalanus* is limited by desiccation and high temperatures on the high shore and in the more southern localities. Direct tests of the temperature tolerances of *Semibalanus* and *Chthamalus* indicate that the latter species is far more tolerant of desiccation and high temperatures, and that the larval stages and newly metamorphosed spat are more susceptible than are adults (Southward, 1958; Crisp and Ritz, 1967; Foster, 1969, 1971a, b).

Southward and Crisp (1956) hypothesized that year to year fluctuations in temperature influenced the relative abundance of *Semibalanus* and *Chthamalus* by changing the intensity of competition between the species. Many details of the geographic distribution of *Semibalanus* and *Chthamalus* were recorded in the 1930's (Moore, 1936; Moore and Kitching, 1939), and these distributions have been studied at the same localities by Southward and Crisp. After a number of warm years *Chthamalus* increased in abundance, and after a number of cold years *Semibalanus* increased (Southward and Crisp, 1956; Southward, 1967; Crisp *et al.,* 1981). They argued that the mechanism might be related to competition for food (Southward and Crisp, 1956, p. 220). Lewis (1964, pp. 251–252) hypothesized that the principal effect of temperature was mediated through competition for space with *Semibalanus*.

The evidence for cold limitation of *Chthamalus* is far less strong than that of heat limitation of *Semibalanus*. Crisp (1950) transplanted *Chthamalus* beyond its northern limit to Whitley Bay in Northumberland on the North Sea coast of England. The individuals survived two winters and produced viable larvae. In the extremely cold winter of 1962–1963, there was no increased mortality of *Chthamalus* in North Wales or in the south or southwest coasts of England (Crisp, 1964). Mortality was higher than usual in south Wales in Mumbles Pier, where there was 25% mortality on horizontal surfaces (Crisp, 1964). During this particular winter a number of species including the commercial oyster and the New Zealand barnacle *Elminius modestus,* suffered extremely high mortality as a result of cold (Crisp, 1964). Southward (1967) stated that the decreases in *Chthamalus* during 1963 were more strongly influenced by the previous cool summer than by the exceptionally cold winter. He suggested that very cold winters were not a major factor controlling the distribution of *Semibalanus* and *Chthamalus* (Southward, 1967). At the northern limit of its geographic distribution, *Chthamalus* is found at the highest shore levels, where the effect of cold air temperatures would be the most severe in winter. If it were not tolerant of cold, *Chthamalus* ought to die in winter at its northern limit,

but it does not appear to do so (*e.g.,* Crisp and Southward, 1958; Lewis, 1964, pp. 251–252). All of these data indicate that direct limitation of the geographic distribution of *Chthamalus* by cold is unlikely.

The northern limit of *Chthamalus* in New England appears to be influenced by temperature as mediated through competition with *Semibalanus.* Post-settlement mortality of *Chthamalus* within the *Semibalanus* zone apparently excludes it from living low on the shore. *Chthamalus* survives in southern New England in the zone where *Semibalanus* dies from desication and/or heat stress (Figs. 1–3). The northern limit of *Chthamalus* occurs where *Semibalanus* no longer dies from desiccation on the high shore (Fig. 5). The absence of adult *Chthamalus* in northern New England is also likely to contribute to a reduced pool of larvae available for settlement, because reproductive populations exist only south of Cape Cod. Failure of larval or juvenile stages has been suggested as setting the northern limit of *Chthamalus* in Scotland (Lewis *et al.,* 1982). In northern Scotland, recruitment declines regularly towards the geographic limit of *Chthamalus* (Lewis *et al.,* 1982; Bowman, 1983). It is likely that this comes about partly because of the progressive restriction of *Chthamalus* by competition with *Semibalanus* to narrower and narrower zones at the highest levels on the shore.

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